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BIOLOGY OF THE THYSANOPTERA[1]

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I. FACTORS GOVERNING LOCAL DISTRIBUTION

Introduction

The Thysanoptera, commonly called thrips, are only beginning to be known, in this country, by systematic entomologists. The systematic knowledge is mostly contained in the monograph of Hinds (1902), a more recent synopsis by Moulton (1911), and a few other papers dealing with new species and with relationships, prominent among which is the work of Jones (1912). Biologically the group is still less known. A considerable number of papers have been issued from experiment stations, describing the life history (egg, larval, pupal and adult stages) and habits of thrips of economic importance. Besides these the principal recent work of a biological nature is a paper of my own (Shull, 1911), on the ecology, method of locomotion, mode of reproduction, and dissemination. The life cycle of most species is still largely unknown.

The first section of this paper is an attempt to carry into further detail the study of the ecology of the Thysanoptera. The first ecological scheme, so far as I am aware, worked out for the Thysanoptera was that of Jordan (1888), who divided thrips into three classes: first, the flower-dwellers; second, the leaf-dwellers; and third, all other thrips (for example, those living on fungi, under wet leaves, under bark of trees, on roots, on lichens, etc.). The inadequacy of this classification, and the difficulty of applying schemes of ecology adapted to other groups of insects, was pointed out in my earlier paper, where I proposed a new scheme, based on my observations in the field. In this scheme, Thysanoptera were divided into two groups: (1) interstitial species, those living in closely concealed situations, as among the florets of composite flowers, or in clusters of young leaves; and (2) superficial species, those living on exposed surfaces, for example, the surface of leaves. The interstitial species were further divided into an anthophilous division (flower-dwellers) and a phlœophilous division (those living under bark scales on trees). The superficial species were either poephilous (on grass) or phyllophilous (on leaves of plants other than grasses). The distinction between poephilous and phyllophilous seemed warranted, since grass-dwellers were found on many different grasses, but rarely on other kinds of leaves.

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Such a classification undoubtedly describes the facts, but does not explain why the habitats named are the ones chosen(?). The factors determining habitat were believed by me at that time to be character of food, and protection afforded. In some species one of these factors predominated, in other species the other factor, while others may have been influenced largely by both. In the light of recent ecological studies, however, the explanation of local distribution in terms of such general environmental factors seems inadequate. Largely owing to the work of Shelford (1911) upon the tiger-beetles, much emphasis is now being placed upon the ecological importance of physiological factors. With a view to relating the distribution of Thysanoptera to the physiology (more specificially, behavior) of the various species, and thus explaining that distribution in more definite terms, the experiments and observations recorded in this paper were made.

This work was done largely at the University of Michigan Biological Station, at Douglas Lake, Michigan, supplemented by observations at Ann Arbor, Michigan, in Ohio and elsewhere.

Facts to be Explained

The following are some of the facts of habits and distribution of the more abundant species for which physiological explanations were sought. Some of these facts are stated in my former paper, some of them doubtless the common property of all thysanopterists; others, so far as I know, have never been recorded.

Euthrips tritici is found almost exclusively *in situations where it is concealed,* as among the florets of composite flowers, in clusters of young leaves, or in almost any close crevice where the tissues are not too hard or tough to be pierced. It appears to make little difference what species of plant is inhabited, provided a concealed situation is available. In the paper cited above (Shull, 1911) I gave a list of seventy species of plant on which *Euthrips tritici* was taken, and I have since collected it on a number of plants not included in that list. But with rare exceptions, it has been found in crevices where it was not readily visible. In related plants, it is always more abundant in those affording concealed situations. Thus, in white clover (*Trifolium repens*) and in red clover (*T. pratense*), this thrips is usually abundant; while on the related yellow, and white, sweet clovers (*Melilotus officinalis* and *M. alba,* respectively), growing along with the red and white clovers, *Euthrips tritici* is usually rare or wanting. The flowers of *Melilotus* are widely separated from one another on the stem, and do not afford concealment (Shull, 1911).

If, while *Euthrips* is in one of these crevices, it is disturbed, as by gently rubbing or pressing the flower, it quickly *comes out of its retreat and crawls rapidly away, or takes to flight.* The larvæ show the same behavior as the adults in this regard, except, of course, that they do not fly.

Anaphothrips striatus is found *usually on grasses* of various kinds, rarely on leaves of other plants. The species of grass seems to make little difference. *Some individuals are found in perfectly exposed situations,* as on the upper side of grass blades, *others more or less concealed* in the rolled up young leaves (Shull, 1911). I have found, however, that among the adults, *those in exposed situations are almost exclusively females, while those in the rolled young leaves are either males or females.* (For the first time on record, the males of this species, as will be shown in the second part of this paper, have been found in considerable numbers.) The larvæ, according to my observations, *may be either exposed or concealed;* the exposed ones are predominantly the older larvæ.

In one of the grasses (*Spartina michauxiana*) on which *Anaphothrips* was found in abundance at Douglas Lake, Michigan, the leaves bear on the upper surface a set of fine, but prominent, ridges running parallel to the axis of the leaf. Adult females and larvæ of *Anaphothrips* on the exposed parts of these leaves were always lodged between the tops of these ridges, and almost invariably *with their heads toward the base of the leaf.* If disturbed, they began to crawl along the crest of one of these ridges toward the base of the leaf. It was possible to force them to turn in the opposite direction, but if allowed to do so they soon turned again toward the base of the leaf, often continuing until they were among the rolled young leaves in the center of the top of the plant.

Anthothrips verbasci is found exclusively on one species of plant, the common mullein (*Verbascum thapsus*). Furthermore, it is rare that a specimen of mullein, of considerable size, is found free from the mullein thrips. Most of the thrips are found *among the florets or seed pods of the spike.* Less commonly they are to be seen on exposed surfaces, as on the leaves or stem lower on the plant; but *these exposed individuals are mostly adults.* The larvæ are usually hidden on the flower spike unless that situation is crowded by a large number of larvæ; and *the larvæ that are occasionally found exposed are mostly nearly fully grown.*

Anthothrips niger was not abundant enough during my stay at Douglas Lake that many observations of its habitat and behavior could be made. One fact, however, is of interest in connection with an experiment to be described. While the adults live mostly on flowers, sometimes concealed, sometimes more or less exposed, the larvæ were always found concealed; moreover, *it was with difficulty that the larvæ could be driven from their retreat by pressing the flowers.* Frequently such vigorous squeezing was necessary to dislodge them that the larvæ emerging were injured; and a flower so treated was often found later to contain numerous dead larvæ. In this respect, the behavior of this species is in considerable contrast to that, for example, of *Euthrips tritici.*

The habitats and behavior described above can be "explained" in large measure if we say, as I at first proposed (1911), that certain species seek protection, or that certain other species have specific food requirements. Thus, it might be said that *Euthrips tritici* seeks safety in crevices, and flees danger when disturbed; that *Anaphothrips striatus* "prefers" grass for food, that it requires as much protection as its commissarial activities permit, and that its habitat and behavior are such as best fulfill these requirements. *Anthothrips verbasci* might be said to be limited to one article of diet, while protection is a minor matter.

This explanation might be acceptable as far as it goes, were it not that no species is immune to attack. I have seen larvæ of *Anthothrips verbasci* frequently captured by various bugs. Heads of mullein where thrips are found nearly always bear bugs of the family Capsidæ, and observations convince me that they prey almost wholly on the larvæ of the mullein thrips. The degree to which they check the thrips was tested experimentally as follows: Two mullein spikes of approximately equal size and equally infected with thrips were selected. The predatory bugs were removed from one of them, after which the spike was enclosed in a thin muslin bag. Two weeks later the bag was removed. The enclosed spike bore a large number of full-grown larvæ, a few had pupated, and many were crawling on the inside of the bag. The spike that was exposed, on the other hand, bore but little over half the number of larvæ that were on the protected one, none were quite full grown, and none had pupated. Since nothing in the climatic conditions (heavy rains, for example) could have caused this difference, it is to be inferred that predatory bugs had devoured the larger larvæ in considerable numbers.

Yet *Anthothrips verbasci,* according to my earlier explanation, "chooses" its habitat almost exclusively in relation to food, protection being a minor consideration.

Can we not explain habitat and behavior in these insects in some way not implying choice, especially choice between conflicting preferences? May we not assume that certain elements of behavior are what they are without reference to their usefulness? If we grant the possibility of an affirmative answer to these questions, the experiments about to be described will have significance.

EXPERIMENTS ON BEHAVIOR

The following experiments were designed to show the reaction of the commoner species of Thysanoptera to what seemed to me the most probable external agents affecting their distribution and behavior, namely, light, contact and gravity. Inasmuch as I was not primarily interested in *how* a given reaction was brought about, but only in its end result, the experiments were rather crude. Refinements were unnecessary, and their omission enabled me to use much greater numbers of individuals than would otherwise have been possible. From ten to forty repetitions of each test were usually made. The experiments are described by species, only representative experiments being given.

Euthrips tritici

Light. Exp. 1.—Adults of this species were placed in a glass tube about three feet long and one inch in diameter, closed at the ends with corks. One end of the tube was turned toward a small window, while the room was rather dimly lighted. All the thrips crawled rapidly toward the window. When the position of the tube was reversed, the thrips reversed their crawling, again going toward the window. The reaction was definite and invariable.

Exp. 3.—A close-fitting sleeve of black building paper was slipped over one half of the glass tube used in experiment 1. The thrips were collected at the exposed end by turning that end for a few minutes toward the window. The covered end of the tube was then turned toward the window. The thrips crawled rapidly toward the light, until they reached the shadow of the sleeve. Here they crawled about, apparently aimlessly, for half an hour an inch or two within the sleeve or just outside it.

Contact. Exp. 1.—When, in the light experiments, the tube was reversed in position as soon as the thrips reached one end, the insects immediately turned toward the opposite end. But if the tube was allowed to rest for some time, the thrips became settled quietly between the glass and the sloping surface of the cork. The tube could then be carefully reversed, and most of the thrips remained lodged between cork and glass for many minutes, some of them for hours. *The positive reaction to contact counteracted the positive reaction to light.*

Exp. 25.—A larva of this species was placed on a glass plate, upon which rested a microscope slide. When the larva in its crawling reached the slide, it came to rest in the angle formed by the glass plate and the edge of the slide. It remained there many minutes until disturbed.

Gravity. Exp. 17.—An adult female was placed in a glass tube which was enclosed in a black sleeve to exclude light, and the tube placed in a vertical position. The position of the thrips was marked with a wax pencil before putting on the sleeve. The sleeve was then removed momentarily at frequent intervals, and the position and direction of crawling of the insect noted. Most frequently it was found lower than the previous position, and crawling downward. This was not always the case, however.

Of other specimens tried, some showed positive geotropism more definitely, some less definitely than the one described. None showed a negative reaction in the majority of cases.

Anaphothrips striatus

Light. Exps. 5 and 7.—Adults of this species were shaken out on a sheet of white paper near a window, and the course of their crawling was plotted as accurately as possible in my notes. Some individuals were decidedly negative to light, crawling directly away from the window every time they were tried, regardless of the direction in which they happened to be headed when they touched the paper. Others were indifferent to light, crawling in various directions. *Most of the males used were decidedly negative to light, females usually indifferent.*

Exp. 10.—Females taken from the exposed portions of leaves of *Spartina michauxiana,* and tested as above, were found in nearly every case to be *indifferent to light. Females from the curled young leaves of the same plants were as a rule negative to light.*

Exp. 6.—Larvæ were usually found indifferent to light, regardless of whether they came from exposed or concealed situations.

Exp. 15.—A single larva taken from the exposed part of a leaf, when placed in a glass tube one end of which was directed toward the window, crawled steadily toward the window. When the position of the tube was reversed, the larva at once reversed its direction. The tube was then placed in a black sleeve to exclude the light, and kept there for an hour. When it was removed, the larva showed for some minutes a *decidedly negative reaction to light.* Later, however, its behavior became indefinite, and *soon became markedly positive. Darkness had apparently temporarily reversed its reaction.*

Contact. Exp. 22.—A female of this species which was negative to light was placed on a sheet of blotting paper. A small square of glass was placed over her, and supported at one edge, so that in crawling away from the window the thrips approached the edge of the glass which was in contact with the paper. She soon became lightly wedged between the glass and the blotter, and came to rest. Blotter, thrips and glass were then carefully turned through 180 degrees so that the negative reaction to light would have led the thrips out of its crevice; but she remained there for a long time. *Positive reaction to contact overcame the negative reaction to light.*

Another female, indifferent to light, was placed under a similar glass. In her random crawling she became wedged between the blotter and glass, and, notwithstanding that the blotter was occasionally turned in the meantime, *remained there several hours, until I lifted the glass.*

Another female, not negative to light, was placed under a similar glass square. She crawled from under it, but happened to crawl against the edge of the microscope slide that supported the glass cover. She settled quickly into the right angle formed by the slide and the blotter, and remained there a long time.

Gravity. Exp. 21.—A female which was indifferent to light was placed in a glass tube, and the tube set in a vertical position. The thrips immediately began to crawl downward. The tube was reversed, and the thrips immediately reversed its direction. A sleeve was placed over the tube to exclude the light, and frequently removed temporarily to observe the position of the thrips. In every case she was found crawling downward.

When the tube was held in an oblique position, the result was the same; the thrips crawled down the slope. If she was already crawling down, a slope of 5 to 10 degrees was found to be sufficient to keep her going in the same direction. But to reverse the direction of crawling, it was necessary to create a slope of about 45 degrees in the opposite direction. The same positive geotropism was shown when the thrips was placed on an inclined sheet of paper; but being here at liberty to fly, she soon interrupted the experiment.

Numerous other females were tried, and all showed positive geotropism, some more promptly than others, but all perfectly definitely. A single male tested showed no definite reaction to gravity. A larva, nearly full grown, subjected to the same tests, showed as definite a positive reaction to gravity as did any of the females.

With the possible exception of the males, therefore, *Anaphothrips striatus is decidedly positive to gravity.*

Anthothrips verbasci

Light. Exp. 4.—Adults of this species, shaken out on a paper near a window, crawled in various directions. *None of them showed any definite reaction to light.*

Numerous larvæ, none of them over three fourths grown, *crawled directly away from the window in every instance.*

Exp. 12.—In this experiment adults from concealed places in mullein spikes were compared with those from exposed situations. They were shaken out on a sheet of paper near a window, and the direction of crawling noted. In every case, *those from concealed situations showed a fairly definite negative reaction to light.* Of those from exposed situations, *two were plainly negative, the remaining ten indifferent to light.*

Exp. 11.—Larvæ taken from concealment in a mullein spike were tested, on a sheet of paper, for their reaction to light. *Those of the smaller sizes crawled directly away from the window.* Those nearly full grown, while on the whole negative, crawled in a more or less devious path away from the window. One reddish larva, which from its color and size must have been *nearly ready to pupate, was especially indefinite in its reaction to light.*

Contact. Exp. 18.—Larvæ of various sizes, which were found to be negative to light, were placed on a blotter under a square of glass supported at one edge, as described for *Anaphothrips striatus.* When, in crawling away from the window, they became wedged lightly between glass and blotter, and came to rest, the blotter with all on it was turned through 180 degrees. The larvæ turned their bodies so that their heads were directed away from the window, but did not crawl away. *The positive reaction to contact overcame the negative response to light.*

An adult tested in the same manner as the larvæ above described did not come to rest under the glass square. But happening to crawl against the microscope slide which supported the glass, the thrips came to rest in the right angle formed by the blotter and the edge of the slide, and remained there a long time.

Gravity. Exps. 13 and 20.—Adults and larvæ were put, one at a time, into a glass tube, which was set in a vertical position, and covered with a black sleeve to exclude light. Some were examined at frequent intervals, others were left half an hour without examination. In every case the thrips were found almost precisely where they were put at the beginning of the experiment. *This species is therefore indifferent to gravity.*

Anthothrips niger

Light. Exp. 2.—The red larvæ of this species were shaken out on a paper near a window, as described in other experiments. In every case the larva *crawled away from the window for a few seconds at first, then slowly turned toward the window, and continued indefinitely toward the light.* Once while the larva was crawling toward the light, I tapped the paper vigorously with a pencil, so that the thrips was lifted slightly from the paper and let drop; *it immediately reversed its direction, crawling from the window,* but in a few seconds turned again toward the light. The paper was jarred frequently, but always with the same result. To show whether the jarring made the response to light negative, or merely reversed whatever the larva was doing at the instant, the tapping was repeated at intervals of one or two seconds.

At the first tap, the larva, which had been crawling toward the window, immediately turned away from the light. Before it resumed its positive response to the light, the paper was tapped again; *the negative response continued.* In this way the larva could be kept crawling away from the light indefinitely. *Disturbance makes the reaction of the larva to light temporarily negative; otherwise it is positive.*

SUMMARY OF EXPERIMENTS

Euthrips tritici, when disturbed, is positively phototropic in both larval and adult stages. It is positively stereotropic, and the stereotropism is stronger than phototropism, at least under certain circumstances. Some individuals appear to be on the whole positively geotropic; others are indifferent.

Anaphothrips striatus.—Adult males are usually negatively phototropic. Females taken from exposed situations are usually indifferent to light, those from concealed situations usually negative. The larvæ are usually indifferent to light, regardless of the kind of place from which they are taken; a single larva that was positive was made negative by keeping it in the dark. Adults are positively stereotropic. The females and larvæ are positively geotropic.

Anthothrips verbasci.—Adults taken from concealed situations are usually negatively phototropic, those from exposed places tend to be indifferent to light. The larvæ are all negatively phototropic, except the full-grown ones, which may be indifferent. The larvæ are plainly positively stereotropic, the adults less plainly so, or not at all. Neither adult nor larva responds to gravity.

INTERPRETATION OF THE EXPERIMENTS IN THEIR RELATION TO DISTRIBUTION AND BEHAVIOR OF THRIPS IN NATURE

With the evidence from these experiments before us, may we not interpret the observed distribution and behavior of the Thysanoptera in nature somewhat as follows? Instead of explaining the fact that *Euthrips tritici* always lives in concealed situations as due to a demand for protection, we may assume that it is due to the strong positive stereotropism of this species—aided in some cases by positive geotropism, where the flower inhabited is upright, but notwithstanding positive geotropism where the flower is inverted. The rapid escape by crawling or flight when disturbed is not due to the fact that this is the best way of avoiding danger, but to the positive reaction to light. Other species avoid danger by going deeper into crevices, because they are negatively responsive to light.

Anaphothrips striatus lives on grasses doubtless because it can not live on any other food, or because the reproductive processes are not stimulated by any other host plant. But their distribution and behavior on the grasses may be explained largely in terms of their reactions to the three agents tested in the experiments. The males usually live in concealed situations on the plants (curled-up leaves) because they are mostly negatively phototropic, and crawl down the leaves until they reach these concealed situations. Females may live either in exposed or in concealed places, for some of them are negative to light, others indifferent. The larvæ are either exposed or concealed, because they are indifferent to light. The eggs from which they hatch are probably laid by negatively phototropic females in the young curled leaves, and the leaves unfold as the larvæ develop; this explains why the exposed larvæ are much larger, on the average, than are those concealed in the young leaves. Perhaps the relation of cause and effect as here stated is reversed, at least for some cases. Concealment—*caused* in one way or another—may lead to negative phototropism, as in the larva which was made temporarily negatively phototropic by being kept in the dark.

The adults are lodged between the ridges on the upper side of the leaves of the grass *Spartina,* not for the sake of protection, it seems to me, but because they are positively stereotropic. Doubtless between the ridges is the place where they can best suck the juices of the plant, but there is no need to assume that they deliberately choose this location in order to get their food most easily. Both adults and larvæ rest on these leaves with their heads directed toward the base of the leaf, and crawl toward the base of the leaf if disturbed, not because protection is most quickly to be found among the curled leaves at the center of the plant, but because the thrips are positively geotropic.

Anthothrips verbasci.—The larvæ of this species live hidden among the flowers of the mullein spike, not because they must get their food there, for they can get it from any part of the plant; nor do they hide there, it seems to me, to secure protection. They remain in these crevices because, excepting the largest larvæ, they are positively stereotropic and negatively phototropic. The adults are sometimes exposed, sometimes concealed, probably because in the former case they are usually indifferent to light, in the latter case negatively phototropic. (Or may they be made negative or indifferent according as they live—for one reason or another—concealed or exposed?)

Thus, while *Anthothrips verbasci* is limited to one food plant, and the food requirements are therefore probably exceedingly important, yet the distribution and behavior of the insects on this plant may be explained without appealing to anything like "choice" in other matters.

Regarding *Anthothrips niger,* I wish to call attention to but one fact. The difficulty with which the larvæ are driven forth from a flower in which they live appears to be due, not to a persistent attempt at concealment, but to the fact that on being disturbed they are temporarily negatively phototropic; if the disturbance is continued, the negative response continues.

The only argument which, it appears to me, could be advanced in favor of assuming that the Thysanoptera choose their locations, instead of adopting simple response to external stimuli as the correct explanation of distribution, is the possibility that they have learned that certain modes of behavior are best suited (for example) to continued safety.

The reply to such an argument is first, that most of my studies on behavior have been made in an unsettled region, where the enemies of thrips incident to civilization are practically wanting, and where even the natural enemies are not abundant. It could hardly be assumed that every individual would learn to avoid its enemies in the course of its short lifetime, yet certain species seem to be invariable in their response to certain agents. Furthermore, many of the larvæ tested in the experiments could have been but a few days old. It is incredible that their reactions should have been, as in fact they were, as definite and invariable as those of older larvæ, if these responses were dependent on experience.

It seems to me, therefore, that the only satisfactory explanation of outdoor behavior and distribution of the Thysanoptera lies in the assumption that they are in large measure the result of responses to simple stimuli, and do not imply any degree of choice.

ORIGIN AND ADAPTIVENESS OF RESPONSES TO EXTERNAL STIMULI

The origin of such responses in Thysanoptera as have been described above is not, I believe, discoverable. Purposeful they most probably are not, as I have shown, if by purpose we mean conscious direction of actions to some end. But adaptive they no doubt are in many cases. Perhaps they are all adaptive, but I confess that my powers of analysis are not keen enough to prove such a view correct. That *Euthrips tritici* is positively phototropic when disturbed is no doubt the cause of frequent escapes from danger. One may even believe the *negative* phototropism of larvæ of *Anthothrips verbasci* to be adaptive, because they are much more sluggish than is *Euthrips tritici,* and could not escape quickly even if they should emerge into the light. They are probably safest, therefore, if, when disturbed, they retire into still deeper crevices. But I am unable to discover the adaptiveness of the response of the larvæ of *Anthothrips niger* to light —at first negative, on being disturbed, but soon becoming positive. Nor can I understand why the males of *Anaphothrips striatus* are more definitely negative to light than are the females or larvæ. These reactions seem to me to be useless.

We need not demand that all of these responses be adaptive, any more than that they be purposeful. Responses have arisen, no one knows how. They have been preserved, and we can but speculate as to the method of their preservation. Natural selection may be responsible for the preservation of the useful, and it may have eliminated responses that were harmful. But other responses of no value whatever, but likewise harmless, may have been allowed to persist, without help or hindrance from selection.

(*To be continued.*)